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Costs of avian incubation

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CHAPTER 1

General introduction

There is large variation in the number of offspring parents produce. This variation in intensity of reproduction not only occurs between individuals of different species, but also between individuals of the same species. As an ecologist, I am interested in understanding this variation in evolutionary context.

Life history theory predicts that parents produce the number of offspring that maximises their personal lifetime fitness. Central to this theory is the idea that organisms have finite resources at their disposal, and thus that investment in one aspect of life (growth, self-maintenance or reproduction) reduces the availability of resources for other aspects (Roff 1992; Stearns 1992). Allocating more resources to offspring production implies allocating less to self maintenance. As a result parents face a trade-off between devoting resources on themselves or on their offspring. Theory predicts that parents should allocate resources in such a way that they maximise their fitness. This prediction can be made when the fitness costs and benefits as a function of this allocation of resources are known. Ideally, for each specific behaviour of an individual – and in this case the intensity of reproduction– the cost and benefits functions should be known to predict the individuals' compromise that would maximise its lifetime fitness.

Reproductive decisions of individuals on the number of offspring to produce have been studied intensively in bird species, because the decision on the allocation of resources to the number of offspring (i.e. clutch size) can be studied experimentally. The number of offspring (eggs or chicks) parents have to care for can easily be manipulated so that the costs and benefits as function of clutch size can be studied. Such an experimental approach is needed, as under natural conditions confounding effects may mask the clutch size-related costs of reproduction. Furthermore, birds have clearly recognizable successive breeding phases (egg laying, incubation and nestling phase). This allows studying the costs of each phase in isolation, and thus in answering the question how important a certain phase is for clutch size decisions.

In this thesis, I will address the question whether selection on clutch size acts during the incubation phase. In the following section I will shortly highlight the work that has previously been done on the subject and I will make clear why I specifically focus on the incubation phase to understand variation in clutch size.

Optimal clutch size

The evolutionary study of clutch size decisions received a major impulse by the early work of the ornithologist David Lack, who, in 1947, constructed a general theory of clutch size in birds. Lack was struck by the fact that clutches are generally small. If the aim of parents is to produce the number of offspring that maximises their own fitness over lifetime then why do they lay so few eggs, sometimes even only one egg, per breeding attempt? Lack also observed that when, during the egg laying phase, eggs were removed from clutches, females just produced another egg to replace the missing one. This implies that clutch size is not limited

by the number of eggs a female can lay. So why then does she limit the clutch to the size observed? Lack (1947) proposed that in altricial (i.e. species that feed their offspring till they fledge) birds, natural selection would favour clutch sizes that correspond to the number of nestlings that the parents can successfully provide with food. The more offspring parents have, the less food will be available for each nestling and some or all of the brood would risk starvation. With his idea, Lack concentrated on the success of offspring of the clutch.

Later studies recognized that counting the number of fledgling of a single breeding attempt is not sufficient to determine parental fitness. When the parent needs to raise a large brood, fewer resources are available for self-maintenance, which reduces the chance to survive and to breed another time. Thus, parents need to trade-off investment in their current brood with potential future reproduction. Therefore, it is important to also determine the survival, and the future reproductive performance of parents, and the recruitment probability of the offspring that fledged successfully (Williams 1966; Charnov & Krebs 1974).

Brood size manipulations

The idea that individuals produce the clutch size that maximises their fitness has been studied intensively by experimentally manipulating the number of young (i.e. further referred to as *brood size*) parents have to rear in the nestling phase (see for reviews Lindén & Møller 1989; Dijkstra *et al.* 1990; Roff 1992; Stearns 1992). The idea behind the performance of brood size manipulations is to select three nests with similar hatch date and brood size; the parents of these nests are assumed to have made the same decision with regard to the timing and intensity of reproduction. Of these three nests, each is randomly assigned to a treatment category; reduced, control or enlarged. Then, very young chicks from one nest are moved to another nest, and parents have to raise the experimentally reduced or enlarged broods till fledging (leaving the nest). Thereby, it is assumed (1) that parents react on the manipulation as if the resulting brood size was the outcome of their own decision (Lessells 1993), and (2) that selection pressures primarily take place during the nestling phase. Subsequently, the fitness of both the parents and their offspring of the experimental broods are compared with those nests that kept their original brood size. Life-history theory predicts that any manipulation deviating from the original clutch size (either up or down) lowers the average number of offspring recruited into the breeding population. Parents with reduced broods are expected to have a lower fitness simply because they raised fewer young than they could have. Parents of enlarged broods are expected to have a lower fitness, either because they are unable to raise all chicks from the enlarged brood or because they are only able to fledge all chicks successfully at the cost of reduction of their own survival, and thus possible future reproduction.

Several studies support this prediction (e.g. Perrins & Moss 1975; Pettifor *et al.* 1988; Gustafsson & Sutherland 1988; Lindén 1990; Tinbergen & Daan 1990;

Pettifor 1993a; Pettifor 1993b; Pettifor *et al.* 2001). Among these studies is the one by Tinbergen and Daan (1990). They performed brood size manipulations in a population of great tits *Parus major* (L.) in the Hoge Veluwe, in the middle of the Netherlands, in the years 1983-1987 (see map Box 1.1). They found that overall fitness (fitness of parents and offspring combined) of the control category was highest, and thus that the observed clutch size of an individual is the one that maximises its fitness (Fig. 1.1). Other studies on the same species elsewhere, however, found negative (Verhulst 1995) or positive selection pressures (Tinbergen & Sanz 2004). In the latter study, Tinbergen and Sanz performed brood size manipulations in another population of great tits in the Lauwersmeer, in the northern Netherlands (Box 1.1), during the years 1995, 1997 and 1998. They found that there was a positive selection pressure on clutch size; parents that received enlarged brood sizes had highest fitness (Fig. 1.1). With the positive selection on brood size, the observed clutch size in the population is expected to increase over time – assuming a genetic component in the variation in brood size. Nevertheless, the mean natural clutch size observed in the population rather decreased than increase over the years (Tinbergen & Sanz 2004). Therefore, the question arose why birds in this population did not lay larger clutches?

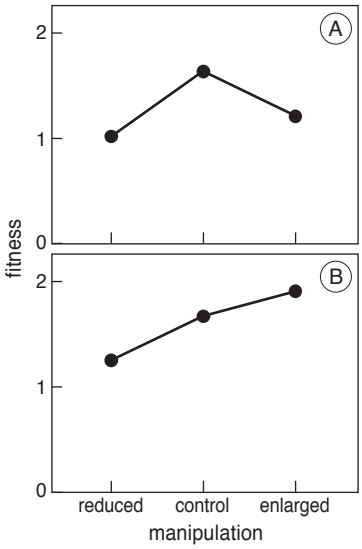

Figure 1.1. Fitness consequences (here defined as the parents that survived and breeding, and the offspring that recruited in the breeding population in the year after manipulation; see Tinbergen and Sanz 2004) of brood size manipulation studied in two Dutch populations (A, Hoge Veluwe; B, Lauwersmeer) by Tinbergen and Daan (1990) and Tinbergen and Sanz (2004), respectively. In the Hoge Veluwe, parents in the control treatment category have highest fitness and thus produce the clutch size that maximise their fitness, while in the Lauwersmeer parents in the enlarged treatment category have highest fitness and thus parents produce smaller clutches than expected on the results of brood size manipulations.

Several reasons have been suggested as to why these experiments led to opposite conclusions even though they were performed on the same species (see discussion in Tinbergen & Sanz 2004). One of the potential explanations is that selection on clutch size does not only act during the nestling phase, but also during other phases in the reproductive cycle, such as the incubation phase (Williams 1996; Monaghan & Nager 1997; Visser & Lessells 2001).

Aim of the thesis

In this thesis I will concentrate on the question whether selection on clutch size acts during the incubation phase and if so whether it could counteract the positive selection as revealed from the brood size manipulations. I study this question within a single system; the population of free-living, nest-box breeding, great tits (Box 1.2) studied earlier by Tinbergen and Sanz (2004). I mainly use an experimental approach (i.e. manipulating the number of eggs in a clutch) in combination with observational data. I estimate the consequences of incubating experimentally manipulated clutches in terms of fitness, physiology and behaviour.

Outline of the thesis

This thesis is divided in two parts: part I focuses on the fitness consequences of clutch size manipulation during incubation (chapter 2 and 3) and on natural selection on clutch size (chapter 4); part II, deals with the energetic and behavioural costs of incubation (chapter 5, 6, 7 and 8). In chapter 9, I summarise the insight that the data have generated and place the costs of incubation in relation to those of both egg laying and rearing offspring.

Part I: fitness consequences

To quantify the costs of incubation as a function of clutch size, we manipulated clutch sizes for the duration of the incubation phase and measured the consequences in terms of fitness for both parents and their offspring in the short and the long term. Chapter 2 provides an overview of studies that manipulated clutch size during the incubation phase, and reveals that most studies have concentrated on measuring the effects of clutch size manipulations in the short term (i.e. within the same breeding attempt). Subsequently, this chapter presents the fitness consequences of clutch size manipulation during incubation that have been performed during three breeding seasons on both the short and the long term. These data show costs of incubation for parents incubating enlarged clutches. These costs are strong enough to counteract the positive selection found with brood size manipulations performed in the same population. Chapter 3 discusses the fact that fitness costs of incubation on offspring performance may arise in two ways: *via parents* or *via eggs*. Due to the manipulation scheme used with these clutch size manipulations, I can disentangled these pathways, which will enhance insight in the mechanism through which clutch enlargement reduces fitness. In chapter 4, we estimate

selection pressures acting on clutch size and lay date in the 'Lauwersmeer' population over 10 years (1994-2003) by relating variation in fitness to variation in both clutch size and laying date. We discuss the fitness estimates obtained in light of those obtained with both the clutch size and the brood size manipulations.

Part II: energetics and behavioural costs

To gain more insight in mechanisms underlying the fitness costs of incubation, we determine the short term consequences of clutch size manipulations by studying the energy management of individuals. Energy is a potential currency that underlies life history trade-offs. The energy expenditure of an individual is thought to be relate to its fitness (Daan *et al.* 1996; Ricklefs 1996). In chapter 5 we describe the phenomenon of delay in onset of full incubation; incubation might be initiated one or more days after clutch completion instead of on the day of clutch completion. As a consequence of this behaviour, the incubation period is delayed and the total reproductive period prolonged. In this chapter, we argue that this behaviour suggests that early reproduction is costly, and thus might influence the timing of reproduction. Studying this phenomenon enhance insight in the reproductive decisions by parental birds. In chapter 6 we focus on the question how much energy females spent during nocturnal incubation in relation to clutch size using a within-individual comparison. Females spent energy at a higher rate when incubating experimentally enlarged clutches than when incubating either reduced or control clutches. We also reveal in this study that ambient temperature is of great importance explaining variation in energy expenditure. In chapter 7 we study whether females incubating enlarged clutches also have higher energy expenditure, when measured over a 24-h period instead of only during nocturnal incubation. We find no substantial difference in daily energy expenditure for females incubating enlarged clutches and those incubating control clutches. In chapter 8 we bring the data of the two previous studies together in combination with data on the time budget of incubating birds, and provide an estimate of how much energy females spent on three main activities performed during the active day; contact incubating (i.e maintaining egg temperatures), rewarming the clutch and foraging. We show that foraging is energetically the most demanding activity.

BOX 1.1 Study area

All studies performed in this thesis were conducted in the woodlots of the Lauwersmeer, in the northern Netherlands (53º20'N, 06º12'E, see map). The Lauwersmeer area was formerly an estuary of the Wadden Sea, but was reclaimed from the sea in 1969. Woodlots were planted starting from 1971, and consisted mainly of young, mixed, deciduous trees of *Populus* sp., *Betula* sp., *Alnus* sp. and *Quercus* sp.. The woodlots studied (see map below) were interspersed with non-breeding habitat consisting of grasslands, reed beds and water.

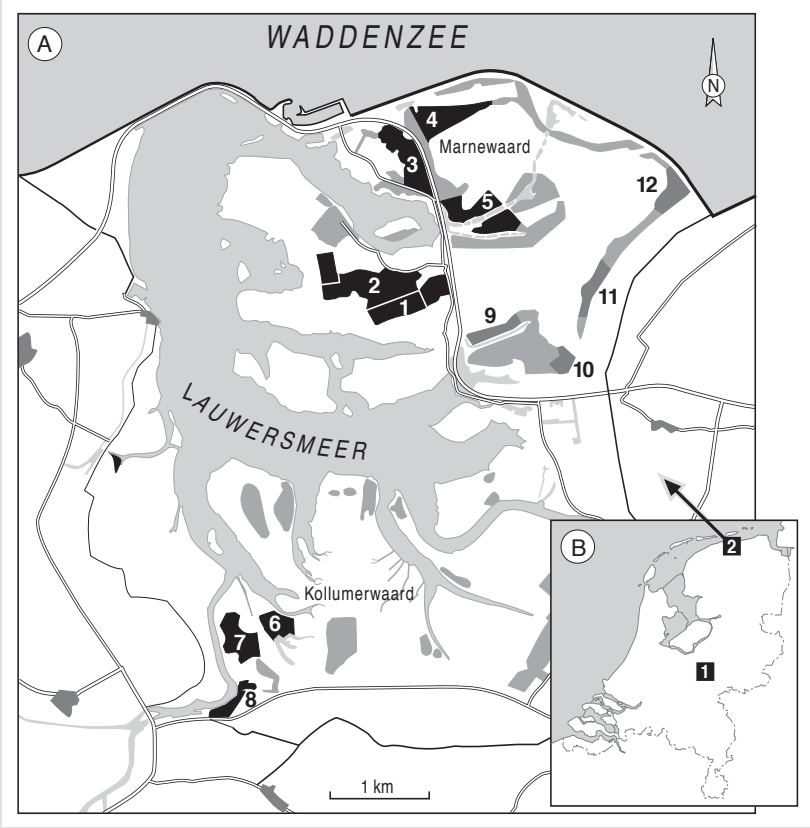

Figure Box 1.1. A) Detailed map of study area the Lauwersmeer with the available woodlots (grey) interspersed with water, reeds and grasslands. The 8 woodlots that have been studied between 1993 and 2004 are marked in black (1-8) and the 4 woodlots that have been added to the study population in 2004 are marked in dark grey (9-12).
B) (inset) Map of the Netherlands with the locations of two main study populations of great tits: Hoge Veluwe (1) and Lauwersmeer (2)

In the Lauwersmeer, no beech crop *Fagus silvatica* (L.) was available as winter food for the great tits. Instead, large numbers of Buckthorn berries *Hippophae rhamnoides* (L.) were available during winter; wintering birds were observed eating those berries. During the nestling phase, nestlings were provided with a diverse diet by the parents. This diet consisted for an important part of caterpillars, but also other species were brought by the parents to their offspring, such as crane flies, black flies, moths, spiders, beetles etc (unpublished data).

History of available nest-boxes in the study area

1980 – A limited number of nest-boxes (61) was available in part of the area; nest-boxes were checked by Rijkswaterstaat and later by the Dutch Forestry

1993 – Study on clutch size decisions in great tits has been initiated by J.M. Tinbergen (RuG)

1994 – The number of nest-boxes was increased to 200, and divided in eight woodlots of different size (6-106 ha). Five of these woodlots were located northeast of the lake, and were isolated from three woodlots southwest of the lake; the maximum distance between nest-boxes was 10 kilometres. Within the framework of studying the process of density dependency on clutch size, nest-boxes were available in either low or high density. Nest-boxes were located at a height of about 2 m off the ground. They were made of wood, and had standard inner size (l x w x h = 12.5 cm x 8.5 cm x 25.0 cm), with diameter of nest entrance 3.2 cm. All nest-boxes were replaced with new ones of the same dimensions in the early spring of 2002.

2004 – 200 nest-boxes were added to the existing set-up; these nest-boxes were divided (50 nest-boxes each) over four woodlots, located in the northeast of the lake.

2005 – Total set-up of nest-boxes has been changed in the frame-work on new study on density dependence, sex allocation and personalities; in total 600 nest-boxes were divided over 12 woodlots (50 nest-boxes each); previous nest-boxes were relocated.

BOX 1.2 Model species

The great tit *Parus major* (L.) was used as model species. The great tit is a small insectivorous passerine that occurs in forest areas in a large part of Europe. In the Netherlands, great tits are resident birds that breed in relatively high densities. During the reproductive season, both the male and female of a pair invest in building a nest. The nest is made of moss and insulated with hair (roe, dog, etc) or fur (rabbit). After nest building, the female lays clutches of around 9 eggs (see below), which she herself

incubates for about 12 days. The great tit is an uniparental incubator: only the female is responsible for the task of incubation. The male may at the most assist their mate by providing food or information where to find food. Both parents provide care to the nestlings that are fully depending on the care of the parents as long as they are in the nest; the nestlings fledge after on average 18 days. After rearing successfully offspring of a first clutch, parents may initiate a second clutch (Kluyver 1951; Perrins 1979).

In the study population in the Lauwersmeer between the years 1994-2003, nest-boxes were occupied by either great or blue tits *Parus caeruleus* (L.). The occupation of nest-boxes by great and blue tits was relatively high (70-90%). Clutches of great tits contained on average 9.3 ± 1.8 eggs (n = 1140). Part of the females (9-51%) produced a second clutch after successfully rearing a first clutch, depending on the year.

Why the great tit as model species?

The great tit was used as model species for various reasons. Great tits normally breed in secondary nest holes, but readily breed in nest-boxes when they are available. Putting up nest-boxes in a forest, therefore, increase the number of available nesting sites for great tits. Besides, these nest-boxes can be located in high densities, thereby, allowing for obtaining relatively high sample sizes. High sample sizes are preferred when studying behavioural variation of individuals in relation to (manipulated) clutch size in their natural environment. An additional advantage of nest-boxes is that they are easy to manipulate (for instance, nest-boxes can be transform into metabolic chamber; chapter 6).

Another reason to study great tits was that individuals of this species show large variation in number of eggs they lay (5-15). As far as I know, great tits do not recognize their own eggs or their own nestlings. Therefore, clutch size and brood size manipulations can be used as tool to study clutch size variation in this species.

Furthermore, since great tits are uniparental incubators, the energetic costs of incubation are likely to be considerably (Williams 1996; Tinbergen & Williams 2002). During the day, the female is faced with a trade-off during the day between spending time on the nest to maintain eggs temperature and spending time away from the nest for self-maintenance (i.e. foraging). Leaving the nest unattended, leads to the fact that egg temperatures fall to ambient temperatures, and thereby slows down development. Letting egg temperatures drop below a certain temperature may be (sub)-lethal (Webb 1987). This trade-off, and thereby the consequences of this trade-off, is likely most pronounced in small passerines, since they cannot store large amount of energy and thus need to forage daily to balance their expenditure.

Moreover, since great tits are resident birds in the Netherlands and site fateful to the breeding site after first settlement (Tinbergen 2005), the more long term effects of experiments on parents and their offspring can be assessed.

PART

Fitness consequences